THE OTIC LABYRINTH AND EQUILIBRATION IN ONE OF THE URODELA (NECTURUS MACULATUS S. MENOBRANCHUS LATERALIS)[1]).

BY

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So far as I am aware no observations on these animals have been published except a brief statement by me in a text-book (1). The experiments were made many years ago and for a number of years I demonstrated them regularly in my class lectures, the animals being easily obtained at Cleveland and the results produced by the lesions studied being very striking and constant. Observations were being carried on at the same time on the relation of the nervous system to the movements of the extremely well developed external gills of this perenni branchiate animal. In two or three cases a brain lesion was combined with destruction of an otic capsule. In all about 20 animals nearly all large specimens obtained from Sandusky on Lake Erie, were employed. The operation was usually performed under ether anesthesia. The animal was held wrapped up in a towel with only the head protruding. If the distance between the posterior border of the eye and the anterior edge of the gills is bisected, and a horizontal line drawn from the point of bisection across the back of the head, a puncture made through the bone a little behind this line and not far from the middle line of the

[1]) Menobranchus or Mud-Puppy or Water-Dog, *Necturus lateralis* (Say) Baird (Jordan's Manual of Vertebrates). Tenney (Manual of Zoology, New York, 1869, p. 316) refers to „the Menobranchus or Mud-Puppy of Lakes Erie and Champlain" as *M. maculatus*, Barnes, and says that „*M. lateralis*, Say, of the tributaries of the Mississippi on the eastern side much resembles the preceding".

„Necturus maculatus s. Menobranchus lateralis... is found in the Eastern half of the United States, chiefly the Eastern part of the basin of the Mississippi and the Canadian lakes. (Gadow, The Cambridge Natural History, 1909, Vol. IX, p. 132").

head, will reach the otic capsule. When put into water immediately after a lesion of one capsule, the animal revolves around its longitudinal axis and always towards the side of the lesion, the observer being supposed to look down upon it as it lies in the normal position.

This rolling movement continues for a longer or shorter time till the animal sinks to the bottom of the tank or gains support at one side. The rolling movements can be started again at any time by disturbing the animal. The movements are similar to those described by Loeb (2) in 1891 in the dogfish. Wilson and Pike (3) have pointed out the uniformity in the effects of labyrinthine lesion in all animals so far studied. In most of the experiments the movements could be elicited as long as the animal lived. The phenomena are best described by giving a few extracts from the protocols of two experiments in one of which the right, in the other the left labyrinth was destroyed.

April 16, 1895. The right otic capsule was destroyed. The animal was at once put into a tank and immediately began to execute rolling movements towards the right. These movements were of considerable strength, for the tail having been caught in the jaws of another Necturus whose cerebral hemispheres had just been removed the latter was forced to roll also for a number of revolutions. After settling to the bottom of the tank the animal with the labyrinth removed came to rest moving its gills, but not so regularly as the other. A great increase in the gill movements is one of the notable effects of removal af the cerebral hemispheres in Necturus.

April 21 to May 2. The animal was frequently observed, and always showed the characteristic rolling movements to the right when caused to move away from the side of the tank. On May 3 it was noticed that the wound was open and the animal rather sluggish, but it still showed the movements of rotation. On May 7 it was found dead, lying on its back. Previously it had always been able eventually to assume the natural position at the bottom or side of the tank.

May 13, 1896. Destroyed the left otic capsule (in Necturus D) under ether anesthesia. On the table immediately after the operation it recovers the normal position perfectly when laid on its back. When thrown into the water it executes rolling movements to the left.

Mar. 20. Still shows rotation to the left round the longitudinal axis when disturbed, especially after being kept out of the water for a few minutes.

Mar. 23. It was found floating on its back and apparently balancing itself with its feet. It still rotates to the left.

Mar. 24. The same characteristic movements.

Mar. 25. It was again seen to rise to the surface and to swim there on its back. When the tail was pinched it dived to the bottom, rolling over and over to the left. It always recovered the normal position (belly-down). It also floated for a considerable time on the surface of the water (belly-down).

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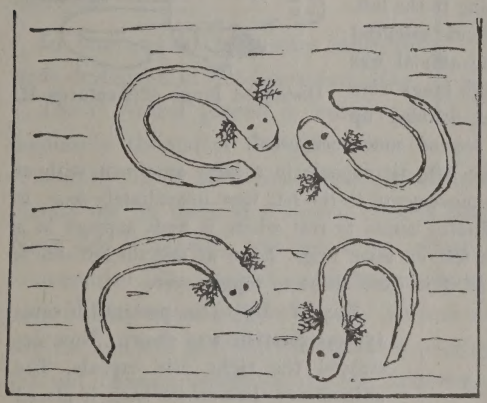
Mar. 27. It was noted that the whole dorsal surface of the head was covered with a fungus growth, which seemed to develop very readily this year on both operated and control specimens. It now floats continuously, is unable to sink, and is evidently dying.

To eliminate the possible effect of the anesthetic on the behavior of the animal immediately after the operation, the left otic capsule was destroyed in a small Necturus without anesthetic. The small operation required only a very brief time. It behaved precisely like the others, being incapable of maintaining the normal position when freely suspended in the water, and rolling round and round, always to the left. These movements were easily elicited on pinching the tail, or if it attempted to move about voluntarily.

Fig. 1.



Positions assumed after destruction of both labyrinths. The animal is supposed to be viewed by looking horizontally at its back through the glass side of the tank. The legs are not shown.

In some of the animals the otic capsule was destroyed on one side, and then after a while that on the other side was destroyed. The destruction of the second labyrinth changed the picture, the rolling movements for the most part disappearing, and being replaced by other characteristic movements the most constant of which was a bending movement of the head towards the tail in a vertical plane first to one side and then to the other while the animal lay on its side, as represented in figure 1. A portion of the protocol of observations is reproduced to illustrate the phenomena observed.

Mar. 20, 1896. Right otic capsule destroyed (in Necturus H.). When put into the water it rotates around a longitudinal axis, always to the right.

Mar. 24. It continues to show the same behavior.

Mar. 27. Still rolls and always to the right, when disturbed, but lies quiet for longer periods than before at the bottom of the tank.

April 1. Found floating on the surface of the water. Very lively when touched. Pinching the tail causes it to roll around the longitudinal axis many times in

succession, always towards the right. It also sinks to the bottom, slanting down with its head on the bottom of the tank (figure 3), and in this position continues to execute the rolling movements to the right. It seems unable to remain at the bottom, and floats up again in spite of its efforts.

April 3. Still floating on the surface. Lively. The characteristic rolling movements to the right are elicited on pinching the tail or touching it with a stick.

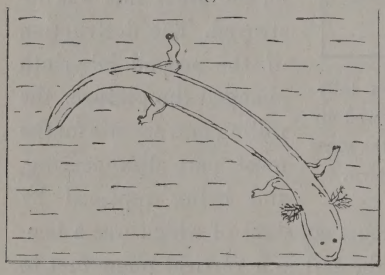
The left otic capsule was now destroyed. The animal still rotates occasionally to the right, but the most characteristic movement now is a bending movement of the head towards the tail, first to one side and then to the other in a vertical plane, as the animal lies on its side (figure 1). The head may come quite into contact with the tail, forming a ring. There is no rolling to the left. This behavior continued without essential change until April 9, when the animal was found dead and still floating. Both lungs were much distended with gas and doubled up (figure 2). The lung vessels seemed much congested.

Fig. 2.

Distended lungs of Necturus H.

March 8, 1897. Destroyed the left otic capsule in a large specimen, without anesthesic. The typical rolling movements to the left were immediately seen. It rotates many times before it finally comes to rest where it finds support in a corner of the tank, or with its feet on some frogs. Even at rest the left side is usually lower than the right, as if it were about to topple over.

Fig. 3.



Necturus B attempting to remain on the bottom of the tank after destruction of one otic labyrinth.

Mar. 12. Up to the present the same typical rotation was shown. Now destroyed the right otic capsule. The animal now lies on its back if placed in that position, the gills moving regularly. They moved very little before the second operation.

Mar. 15. It will now recover the normal position if placed on its back in water in a vessel with a slightly convex bottom, but not if the bottom is horizontal, although with a very little aid it will do so in this case also. The gills are not moved more than by a normal animal. It is very lively when touched and moves about a good deal. It has no tendency to rotate when touched or pinched. A few hours later when placed in a tank with a flat bottom it recovered the normal position without help after a very short effort. This was repeated twice.

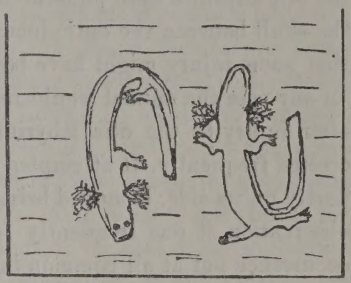
Mar. 16. It is still able after a short struggle to regain the normal position when placed on its back in the tank with the flat bottom.

Mar. 17. When stimulated it executes the movements shown in figure 1;

lying in the water with its lateral surface downwards it quickly brings its mouth to, its tail first on one side and then on the other, forming a circle when the mouth has reached the tail.

Mar. 18. It can no longer sink, but lies on the surface of the water, sometimes on its back, sometimes on its left side. The vibratory movements (fig. 1) are exceedingly well marked, especially when it tries to reach the bottom. The gills are not moved much.

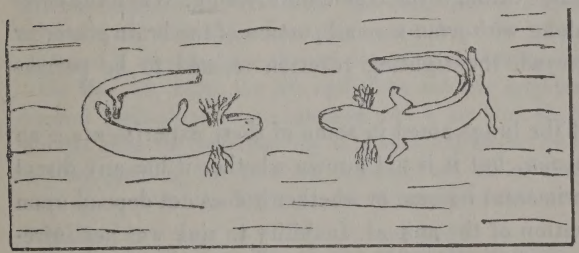
Fig. 4.



Mar. 22. Died. The fungus noticed last year was present on the head and gills, and also a patch on the side. The necropsy showed that both otic capsules had been destroyed.

In one animal both otic capsules were destroyed at one operation (May 7, 1895). When placed in water immediately thereafter the gills moved constantly, as in an animal deprived of its cerebral hemispheres. When placed on its back the animal showed little inclination to right itself. Next day it seemed restless. When stimulated it moved as if turning somersaults (fig. 4), but came to rest again always in the normal position. When at rest there was no obvious difference between it and the control and the gill movements were now not conspicuous. Its behavior did not change much during the time it continued to live, except that on the last day stronger stimulation was necessary to elicit the movements. It died on the fifth day after the operation.

Fig. 5.



The „somersault" movements are far less common than the lateral twisting movements already described, which were also seen in this animal. Bending movements in the horizontal plane, the back first becoming convex and then concave, as the animal lies on its side (fig. 5) were rarely observed.

The twisting movements (fig. 1), as if it were attempting to catch its tail, first to one side and then to the other were seen in an animal in

which both otic capsules were punctured at one operation. The movements were elicited easily whenever the animal was caused to swim, certainly for 11 days after the operation. While it was executing these movements it might be swimming in a circle on its back. During the remaining 7 days for which it lived observations were not made. Before the otic capsules were punctured an attempt had been made to trephine the skull between the optic lobes and the cerebellum, and it is possible that some injury might have been inflicted on the brain in this region. In any case the animal would lie on its back after the operation, which after injury to the otic labyrinths alone it will not do. The head was erected frequently. It attempted to right itself, and could do so if placed partly on its side. It moved briskly if pinched. For the time it was under observation it was frequently found in the tank lying on its back, an occurrence not at all common in these experiments. Although both otic capsules had been punctured it was seen *post mortem* that the otoliths were apparently still in the normal position.

Lesions of the cerebral hemispheres were not associated with the production of forced movements, but with a greatly increased activity of the gills. If only the cerebral hemispheres were removed, the animal would generally right itself when laid on its back. Sometimes this reaction, present immediately after the operation and perhaps for a day or two longer, would disappear later on, possibly because of further injury to the brain caused by the blood clot, which always filled up the wound, or by entrance of water through the collodion dressing. When the cerebral hemispheres, along with even a small portion of the brain posterior to them, were destroyed, the righting reaction seemed to be permanently lost.

The distention of the lungs noted in some of these experiments is an interesting phenomenon, but it is not known whether it has any direct relation to the experimental lesions, or whether it does not depend upon the general deterioration of the animal. Inability to sink was not infrequently seen a day or two before death. In some cases at any rate it seemed clearly associated with the accumulation of an excessive quantity of gas in the lungs. There is reason to believe that in these animals the lungs play only a very subordinate part as respiratory organs. Be this as it may, they must aid to a greater or less degree, according to the amount of gas contained in them, in balancing the weight of the animal when immersed, like the swimbladder in fishes, and therefore in main-

taining equilibrium. Such lesions of the mid-brain as were studied did not prevent the animal from righting itself when laid on its back. The gill movements were not affected as after removal of the cerebral hemispheres. On the other hand, movements of rotation around the longitudinal axis were not uncommon after a unilateral lesion, and in righting itself when placed on its back the animal usually rolled towards the side opposite to the lesion, whereas after destruction of one otic labyrinth the direction of rotation is always towards the lesion, the observer being supposed to look down upon the animal lying in the normal (belly-down) position. On the whole this agrees with LOEB's (2) results on dogfishes. But my experiments on the mid-brain were few, and chiefly concerned with the influence of lesions of the optic lobes on the righting reactions of the animal when placed on its back. And LOEB found that in the cartilaginous fishes studied by him lesions of the roof of the mid-brain did not seem to cause disturbances of orientation, as did injury to the base of the mid-brain. Also in some of my experiments two operations were done at different times, and the extent of the first lesion could not be controlled by *post mortem* examination.

On March 9, 1896, the left optic lobe was almost completely destroyed and the posterior two-thirds of the left cerebral hemisphere also (in Necturus C). Immediately after the operation it righted itself when placed on its back in water. The jaws snapped vigorously. The righting reaction was always present during the 18 days for which the animal lived. The gills were moved comparatively little, which is quite different from their behavior after excision of both cerebral hemispheres. At death the whole dorsal surface of the animal was covered with fungus growth. The brain, kept in 80 per cent alcohol, when examined 7 months later showed numerous cholesterin crystals.

On Mar. 23, 1896, the left optic lobe and the neighboring region of the left cerebral hemisphere were cauterised with a hot wire (in Necturus I). For a few minutes after the operation the animal would lie on its back in water if placed in that position, but later on it would not do so, always righting itself by rotating towards the right around the longitudinal axis, i. e. the right side came up.

On March 26, however, 3 days after the operation, it was noted that it righted itself by a rotation in the opposite direction, the left side coming up; and on March 27, it was observed that the righting reaction took place as often in one direction as in the other. It is possible that some recovery of tissue partially injured by the cautery was occurring.

On Mar. 27, the wound was opened and more tissue was destroyed in the region of the optic lobes. It was tried repeatedly during the operation whether the animal would lie on its back, and tissue was destroyed until the power to

recover the normal position seemed just to be lost. Next day the animal was lively but did not right itself in the water when placed on its back, although it was found in the morning in the natural position, in which it had been placed the previous evening. When taken out of the water and placed on a table it became extremely lively in a minute or two, and easily righted itself when laid on its back.

On March 30 it was found dead. The left optic lobe was almost completely destroyed and also the posterior half of the left cerebral hemisphere.

A quite similar experiment was made on another specimen (Necturus K) and with practically the same results. The righting reaction was not lost. In regaining the normal position when placed on its back in water during the first days it righted itself by rotating to the right around the longitudinal axis. When disturbed it rotated completely several times before coming to rest, just like an animal with a unilateral labyrinthine lesion, but in the opposite direction. After a few days it was seen that in righting itself the animal occasionally rotated to the left, and a few days later still it rotated as often to the left as to the right.

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(2) Loeb, J.: *Pflüger's Arch.*, 1891, Bd. 50, S. 66.

(3) Wilson, J. G. and Pike, F. H.: *Phil. Trans. Roy. Soc.* (London), 1912, Series B, Vol. 203, p. 157.

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